

SEASONAL PHENOLOGY OF *BATTUS PHILENOR* (L.) (PAPILIONIDAE) IN CALIFORNIA¹

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ABSTRACT. The pipevine swallowtail butterfly, *Battus philenor* (L.), has a flight season extending over more than nine months (February to November) in central California. The major flight occurs primarily in April and is derived from overwintering pupae in diapause. This flight is followed by a partial second generation, consisting of 9-39% non-diapause first generation offspring. A subsequent temporally scattered flight, representing a third generation, is partially derived from earlier season diapausers emerging in summer and fall. Under field conditions, pupal diapause intensity progressively declines through fall and early winter. Pupal photoperiod response and diapause end by mid-winter. There is no sex ratio distortion in either second brood or summer-fall emergers. Spring field emergence of males tends to precede females, suggesting differences in relative rates of post-diapause development.

A necessary step towards an understanding of the population dynamics and distribution of Lepidoptera is to examine their seasonal phenology or timing of recurring periods of activity and dormancy in relation to key environmental factors. For species with a diapause phase, the appropriate timing of the onset, maintenance, and termination of diapause, followed by postdiapause development and resumption of reproductive activity is vital to the successful adaptation to their environment.

The pipevine swallowtail, *Battus philenor* (L.), has an extended flight season in central California with adult activity recorded from February to November (Opler & Langston, 1968; Shapiro, 1974). Little, however, is known about how the flight season is related to the population dynamics and pupal diapause of this species. Shapiro (1975) suggested that the long flight season and apparent multivoltinism results from reproduction by a non-diapause fraction of each generation. Thus, each generation may be a mixture of both continuous developers and individuals that undergo an aestivo-hibernal pupal diapause (Masaki, 1980) and emerge the following spring.

In this paper we examine the phenological "strategy" or timing of the active and diapause states of *philenor* as they relate to the annual periodicity and variability of the central California habitats. Specifically, we estimate the number, timing, and derivation of annual broods and determine when diapause terminates under field conditions.

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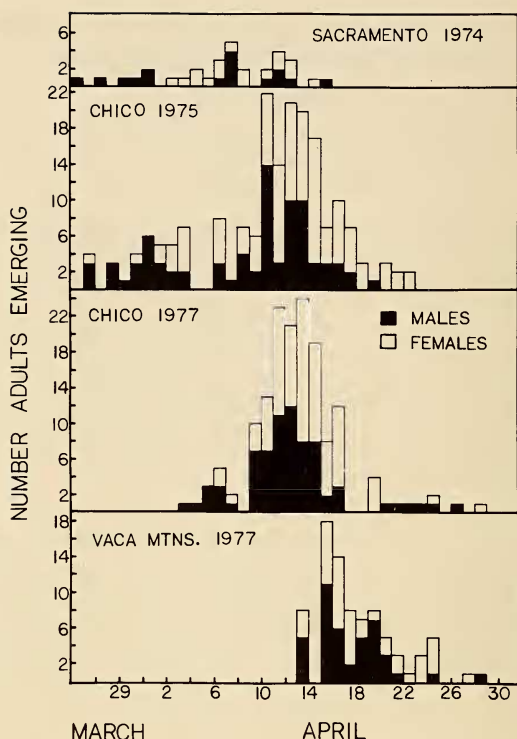


FIG. 1. Spring emergence of first brood adult *B. philenor* from overwintering pupae.

MATERIALS AND METHODS

We collected living material from the following populations: Chico, Butte Co., CA, 39°42'N (latitude), 60 m (altitude); Davis, Yolo Co., CA, 38°30'N, 16 m; Vaca Mountains (from Mix Canyon to Solano Lake, approx. 7 km SW Winters), Inner Coast Range, Solano Co., CA, 38°25'N, 50–300 m; Sacramento, Sacramento Co., CA, 38°30'N, 15 m.

To estimate diapause incidence and adult emergence under field conditions, we sampled first generation final instar larvae and prepupae from the Davis, Chico, Vaca Mtns., and Sacramento populations during mid-May to mid-June from 1974–1976. Samples were maintained outdoors, at Davis, on cuttings of the foodplant, *Aristolochia californica* Torr., in large (46 cm side) screened cages. Completion of feeding and pupation occurred within one week of collection. Both larvae and pupae were sheltered from rain but exposed to normal seasonal variations of temperature and photoperiod. Individuals were labelled with col-

TABLE 1. Percent non-diapause of first brood *Battus philenor* (A) and percent of adults emerging in July, August, or September from first brood diapause pupae >30 days old (B). Number in parentheses is sample size; NS = not sampled.

	1974		1975		1976	
	A	B	A	B	A	B
Davis	25.0 (4)	—	23.1 (26)	—	NS	—
Vaca Mtns.	39.0 (141)	3.2 (93)	27.4 (168)	—	15.8 (146)	5.7 (123)
Chico	NS	—	8.8 (616)	3.7 (135)	14.2 (558)	21.3 (230)

lection and pupation date and monitored daily for adult emergence and sex. We used the same collection, storage, and recording methods to study the timing of spring adult emergence the following year.

The termination of diapause, or completion of diapause "development" (Beck, 1980), can be studied in photosensitive species by determining the date at which photoperiod no longer influences the rate of morphogenesis; i.e., when morphogenesis is primarily a function of temperature and proceeds at a rate similar to that of non-diapause individuals (Tauber & Tauber, 1976). Since *philenor* pupae are photosensitive, with the rate of diapause development inhibited under short-day photoperiods and increased under long-day photoperiods (Sims & Shapiro, 1983), we were able to study field diapause development as follows: Pupae, derived from final instar Chico larvae collected on 11 June 1976, were maintained outdoors through summer and fall in Davis. At monthly intervals from 20 November 1976 to 20 February 1977, samples of pupae were transferred from their outdoor location to LD10:14, LD15:9, and a natural photoperiod (greenhouse) at approx. 23.5°C and monitored for emergence. Data were analyzed using ANOVA procedures and Duncan's Multiple Range Test (DMR) for significance of differences between means (Sokal & Rohlf, 1969).

RESULTS

Our 1974–1977 adult emergence data from overwintered pupae show a unimodal peak of spring emergence during the second and third weeks of April (Fig. 1). This peak coincides with a period of rapid *Aristolochia* growth.

Non-diapause pupae and resulting adults obtained from field-collected first generation larvae provided an estimate of the magnitude of the second generation. The second generation ranged from less than 10% to almost 40% of the surviving first generation pupae (Table 1). The Vaca Mtns. population (1974–1976) illustrates that considerable yearly variation may occur in second generation size. Mortality of first generation pupae was low, ranging from 5–10%.

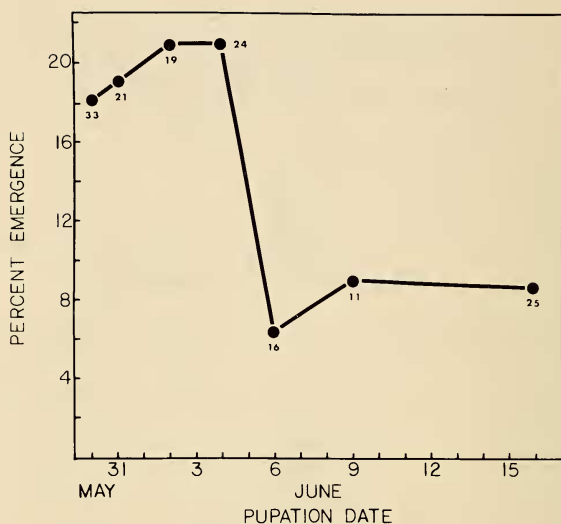


FIG. 2. Mean pupation date and percent adult emergence of *B. philenor*. Vaca Mtns. population; spring 1976. Numbers indicate sample size.

Pupae from the Vaca Mtns., over 18 days in late spring, 1976, showed a marked decrease in adult emergence with increasing pupation date (Fig. 2). Increasing diapause was not correlated with temperature (daily mean or minimum) but may have been related to host-plant quality which deteriorated visibly (increased leaf toughness and decreased succulence) during this period. A seasonal increase in pupal diapause is a possible bias in our estimation of second brood magnitude despite using larvae collected from mid-May to early June. Thus, samples taken relatively early in the season might overestimate, while late-season samples may underestimate non-diapause among first-brood individuals.

From first generation pupae in aestival diapause (>30 days post-pupation), a small number of adults continued to emerge in July, August, and September (Table 1). The extent to which this scattered flight is augmented by a third generation is unknown, but since relatively few larvae were observed on *Aristolochia* after June, the third and any subsequent broods are presumably quite small.

Diapause in the field was considered terminated when there was no significant difference in time (days) to adult emergence among the short-day, long-day, and natural photoperiods at 23.5°C to which pupae were transferred at monthly intervals from November to February (Tauber & Tauber, 1976). Using this criterion, pupal diapause ends

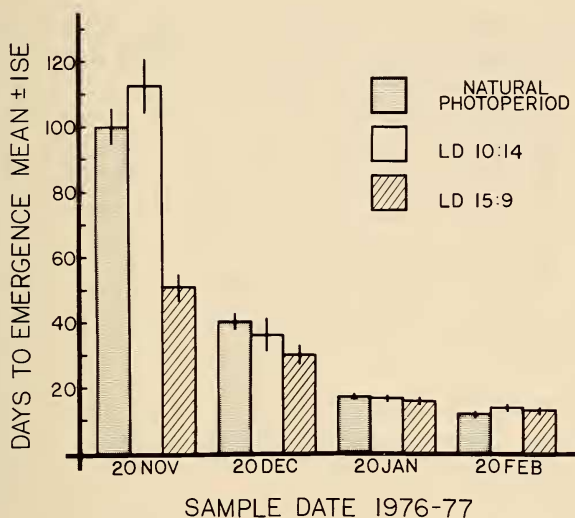


FIG. 3. Adult emergence from diapause *B. philenor* pupae maintained outdoors prior to 23.5°C exposure at the indicated photoperiod.

during the 30-day period following the winter solstice (Fig. 3). Under each photoperiod, adult emergence time was significantly less in January than in December samples, while emergence times for January and February were similar (DMR test, $P < 0.05$). Pupae from the November and December samples displayed a distinct photoresponse. November pupae at LD15:9 emerged significantly sooner than those at LD10:14 or natural photoperiod, while December pupae at LD15:9 emerged sooner than those under a natural photoperiod.

There was little departure from a 1:1 sex ratio among either second brood (51.5% ♂♂, $n = 264$) or summer-fall emerging individuals (51.6% ♂♂, $n = 64$). A comparison of cumulative numbers of males and females present after the onset of seasonal emergence shows that males tend to emerge somewhat before females (Fig. 4).

DISCUSSION

Central California populations of *philenor* have two major flights each year. The first and largest flight occurs in March and April and derives from the unimodal emergence of adults from overwintered pupae. Most first brood pupae undergo an aestivo-hibernal diapause (Masaki, 1980) and overwinter. Some individuals emerge to form a partial second generation, the magnitude of which shows both inter- and intrapopulation variation (Table 1). There is evidence suggesting

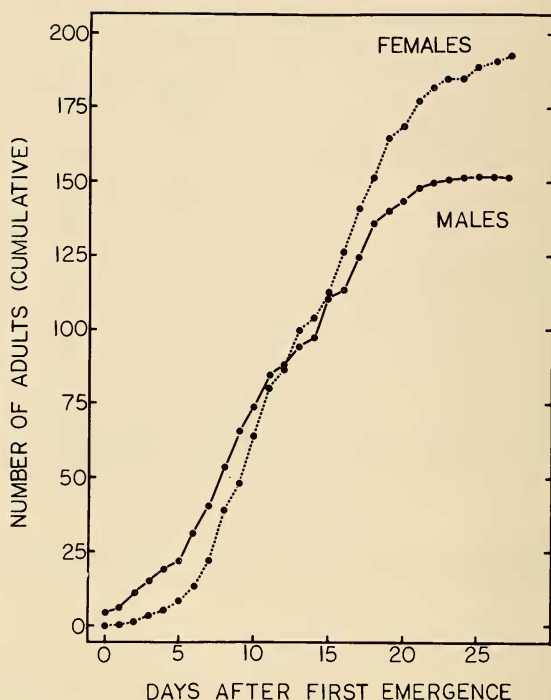


FIG. 4. Cumulative emergence of spring generation *B. philenor* adults from overwintering pupae, by sex. Chico, CA population; combined emergence of 1975 and 1977.

a positive relationship between the pupation date of first brood larvae in the field and diapausing frequency (Fig. 2). The increase in diapause parallels the visually-determined seasonal decrease in young succulent *Aristolochia* foliage available for larval consumption. Rausher (1981) documented a similar seasonal decrease in the quality of *Aristolochia* from Texas. In Texas, the increase in the sclerophyllization (=increased leaf toughness and decreased nitrogen) of *A. reticulata* (Nutt.) between March and May led to poorer larval growth and increased larval dispersal of *philenor*.

Emergence of adults from the diapausing first generation age-cohort is divided between summer-fall and the following spring. The summer-fall emergers contribute to the scattered flight of *philenor* from July to November in California. The emergence polymodality represented by the aestivo and aestivo-hibernal diapausers of the first generation *philenor* age-cohort does not conveniently fit into any of the phenological categories suggested by Waldbauer (1978). Despite this, it is not a

unique example. Among other papilionids, *Papilio maacki* Fenton (Ichinosé, 1974), *Eurytides marcellus* (Cramer) (Scudder, 1889), and some populations of *Papilio machaon* L. (Wiltshire, 1957) show similar discontinuity in pupal diapause duration as does the noctuid moth, *Barathra brassicae* L. (Masaki, 1956; Dolidze cited in Danilevskii, 1965). The reproductive success of *philenor* adults emerging in summer-fall is unknown. Since females oviposit exclusively on tender growing shoots and first instar larvae can only feed on these, opportunities for summer reproduction are usually limited. Following the onset of fall rains in September and October, a small amount of new *Aristolochia* growth may become available, and we have found both ova and final instar larvae on this growth in late October.

Diapause development in *philenor* is completed before midwinter (Fig. 3). No photoresponse was found in pupae sampled one month after the winter solstice; the development rate of pupae at this time was similar to non-diapause pupae at the same temperature. It is most likely that morphogenesis and adult emergence in the spring following diapause termination are functions of temperature accumulations above a minimum temperature developmental threshold.

Previous observations that individuals of later broods are primarily males (Fee, 1979) are not supported by our results which show no sex-ratio distortion among either second brood or summer-fall emergers. The only evidence for sex-related phenological differences was obtained from adult emergence from overwintering post-diapause pupae. Females lag slightly behind males in emergence times, suggesting a greater heat unit requirement among females for completion of development.

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